Fruit fall in tropical and temperate forests: implications for frugivore diversity

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Abstract

There have been few attempts to compare fruit productivity throughout the world, although this is indispensable for understanding the global variations in frugivore diversity. The purposes of this study are (1) to reveal the patterns in fruit fall in tropical and temperate forests, (2) to examine the environmental factors (location, climate and total litterfall) affecting these patterns and (3) to assess the effect of fruit fall on frugivore diversity by using bird and primate data. Fruit fall was compared among 53 forests, from around the equator to the cool-temperate zone at 62ºN, in Asia, Africa, North and South America and Australia. Average ±SD of fruit fall (kg/ha/year) was 454±258, in tropical and 362±352 in temperate forests. Fruit fall was exceptionally high in Australia (812±461). When Australia was excluded, fruit fall significantly decreased with increasing absolute latitude and altitude, and fruit fall in tropical forest was 1.7 times larger than that in temperate forests (265±227). Total litterfall affected fruit fall significantly, explaining 32%, 28% and 64% of the variations of fruit fall in the entire data, tropical data, and temperate data, respectively. The fruit fall/litterfall ratio did not differ between temperate and tropical forests but was significantly higher in Australia than in other regions. Among climatic parameters (annual temperature, precipitation, actual evapotranspiration), a positive relation was found between temperature and fruit fall in the entire dataset and within temperate forests. Fruit fall seemed to explain the temperate/tropical difference in frugivorous primate diversity to some extent, but not for frugivorous bird diversity. This study shows that the difference in fruit fall in tropical and temperate forests is smaller than that in frugivore diversity, and that it could explain at least part of the frugivore diversity.

42 Keywords: fruit; litterfall; tropical forest; primate; productivity

43

Introduction

There is a general tendency for species richness to decrease with increasing latitude, both among animals and plants (Eeley and Lawes 1999; Badgley and Fox 2000; Stevens and Willig 2002; Hillebrand 2004; Takyu et al. 2005). It has been argued that the number of species increases with the total number of individuals in that community because the probability of local extinction of a species is affected by its population size (Turner 2004). If this is true, species richness is positively correlated with the carrying capacity of the habitat, and thus it should have a positive correlation with energy availability, productivity and climate. In fact, positive correlations between energy availability or productivity and species richness have been reported for plants (Pärtel et al. 2007), ants (Kaspari et al. 2004), and birds (Evans et al. 2006). At the same time, species richness may also be affected by evolutionary history. In temperate regions, the number of species may have decreased during the glacial/post glacial climate change, and thus species diversity is smaller even if productivity is the same as in the tropics. The productivity-diversity relationship in plants is linear in the tropics but unimodal in temperate regions, suggesting that plant species richness does not increase in highly productive situations in temperate regions (Pärtel et al. 2007). Abrupt decreases in diversity from tropical to temperate regions have been reported in many taxa, including primates and birds (Eeley and Lawes 1999; Turner 2004).

Most of the studies on latitudinal gradients of species richness have been comparisons among higher-level taxonomic groups, such as mammals or birds. However, when examining finer-scale taxonomic or trophic groups, it is necessary to analyze their food abundance directly, rather than using

productivity or climate as a proxy for resource availability. In the case of frugivores, it is essential to estimate fruit production. For example, fig species diversity affects the diversity of sub-Saharan frugivorous birds, while the effects of productivity and climate affect frugivore diversity only indirectly through fig diversity (Kissling et al. 2007). There is no positive relationship between forest productivity and frugivorous primate abundance (Janson and Chapman 1999), but fruit production assessed by fruit fall positively correlates with frugivorous primate diversity and biomass (Stevenson 2001). A recent study on the global pattern of fruiting phenology (Ting et al. 2008) revealed that fruiting season lasts longer in tropical than in temperate areas. In order to clarify the difference in frugivore diversity, however, it is necessary to compare not only fruiting seasonality but also fruit production. Different methods have been used to estimate fruit production in temperate and tropical regions (Herrera 1985). In temperate forests, fruit production has been estimated largely by counting the number of fruits in branches. This is clearly impractical in tall and densely vegetated tropical forests. Fruit production in tropical regions is usually studied by fruit fall, but systematic comparisons of fruit fall have rarely been made. Moles *et al*. (2009) is one of the few exceptions, and they estimated latitudinal cline in seed production. They derived seed production by multiplying average seed mass and average seed rain density at each latitude, concluding that seed production at the equator is between 19 and 128 times more than that at a latitude of 60°. Their tentative conclusion that there is such a big difference between tropical and temperate regions needs to be tested by direct data.

In this paper, we review data on fruit fall in forests, from around the equator to the cool-temperate forest at 62°N, in order to clarify the difference in

fruit production between temperate and tropical forests. We explore the effect of three kinds of habitat characteristics on fruit fall: location (latitude, altitude, and region), climate (temperature, precipitation and actual evapotranspiration), and primary production (assessed by total litterfall). Because fruit fall data are not easily available, this analysis offers a way to estimate it from more easily measured variables. Finally, using part of the reviewed fruit fall data, we examined whether fruit fall explains the difference in diversity of two groups of frugivores (primates and birds) between temperate and tropical regions. We examine whether the difference in frugivore diversity between tropical and temperate regions exists even when the effect of fruit fall is controlled. The presented review provides important baseline information for discussing the effects of fruit availability on the latitudinal gradient of frugivore diversity.

Methods

Fruit fall

In this study, we define ‘fruit’ in an ecological sense. We classified cones, arils, and other seed-bearing structures of conifers as fruits because most studies of litterfall do not segregate these organs from fruits of angiosperms.

Data on fruit fall biomass were reviewed from the literature. We used the ISI Web of Science (http://apps.isiknowledge.com/) to search for relevant literature. On February 19, 2010, we conducted our search by inputting the keywords ‘litterfall’ and ‘fruit AND fall’; these searches found 1,207 and 1,504 results, respectively. We read the abstracts of the papers and gathered those papers when that referred to the composition of litter. If we judged that the study did not cover more than a year or did not collect litter in a systematic way,

we did not use the paper. We also gained data from the reviews done by Bray & Gorham (1964) and Saito (1981). We compared fruit fall on a dry weight basis. If only data on wet weight were available, we estimated dry weight assuming that dry weight is 29.5% of wet weight, which is the average value of seven temperate sites (Herrera 1985). This value might differ between the temperate and tropical forests; however, in a tropical forest of the Danum Valley, Borneo, dry weight of fruits was 29.1% of the wet weight (average of 310 fruits, G. Hanya, unpublished data), a similar value to that in temperate forests. If only a summed value of the total reproductive organs (fruits and flowers) was available, we estimated fruit weight assuming that fruit weight is 63% of the weight of total reproductive organs, which was used in the estimation of fruit fall in Central and South America (Stevenson 2001). This value is not so different from those in Yakushima, southern Japan: (53%, average of five plots; G. Hanya & S. Aiba, unpublished data). Furthermore, we included three old secondary forests but did not include plantation forests. Data were available from 53 sites, with latitudes of 36°S-62°N, covering Africa (6), Eurasia (15 Asia and 6 Europe), America (16 Central and South America and 2 North America) and Australia (5), two Canary Islands sites, and one New Zealand site. Using tropics of Cancer and Capricorn (N/S 23°26') as the borders between the temperate and tropical zones, the number of sites was 25 in tropical and 28 in temperate forests. See Table 1 for detail of the study sites.

For each study site, we collected the following information: (1) latitude, (2) longitude, (3) altitude, (4) region (Africa, Eurasia, America, Australia, Canary Islands and New Zealand), (5) annual average temperature, (6) annual precipitation, (7) actual evapotranspiration, and (8) annual total litterfall.

144 Factors from (1)-(4) are on location, (5)-(7) on climate, and (8) on primary
145 production. The direct effect of longitude on fruit fall was not assessed; it was
146 used only to calculate the inter-site distance in order to correct the spatial
147 autocorrelation (see next paragraph). We used the absolute values of latitude
148 in the analysis of its effect on fruit fall; therefore, northern and southern
149 hemispheres were treated equally. Data on annual average temperature and
150 annual precipitation were derived from original literature whenever possible.
151 When not available, data were cited from the nearest meteorological station,
152 using the database 'World Climate' http://www.climate-charts.com/. In the case
153 where the altitude of the meteorological station differed from the study site by
154 more than 200 m, we corrected the temperature value by assuming that the
155 temperature lapse rate is 0.6°C/100 m (Martyn 1992). Data on actual
156 evapotranspiration were cited from Ahn & Tateishi (1994), downloaded from the
157 United Nations Environment Programme geodata repository
158 (http://www.grid.unep.ch/data/data.php, dataset GNV_183) and presented at a
159 0.5º resolution. Location and climate factors were available for all of the study
160 sites, but the litterfall data were available for only 37 sites.
161 We examined the data for five cases: (1) entire, (2) temperate and
162 tropical excluding Australia, (3) tropical, (4) temperate, and (5) temperate
163 excluding Australia. We analyzed data excluding Australia because we found
164 that there were apparent outliers there (see results). In addition, we examined
165 the effects of location, climate, and litterfall factors separately because we could
166 assume that these factors were interrelated (location determines climate, and
167 climate determines litterfall).
168 We examined the global relationships between location, climate and

169 litterfall factors and fruit fall using generalized least squares (GLS) regression.
170 GLS models are similar to general linear models (GLM), except that their
171 estimates of standard errors and type-I errors are more realistic in the presence
172 of spatially correlated residuals (Dormann et al. 2007). GLS models also
173 prevent clusters of sites from exerting undue (pseudo-replicated) influence on
174 estimates of beta coefficients, which may be an important consideration if study
175 sites are not uniformly distributed in space (Ting et al. 2008). In applying GLS,
176 we first compared the fit of three common variogram models: the 'spherical',
177 'Gaussian', and 'exponential' functions in the full GLS models using all of the
178 predictors for each analysis (e.g. region, absolute latitude and altitude in the
179 case of analysis of location). Second, the function having the smallest AIC
180 (Akaike's Information Criterion) was used for subsequent analysis. Finally, we
181 decreased the number of predictors until we obtained the best-fit model having
182 the smallest AIC. GLS models were fit using the 'gls' command of the 'nlme'
183 package in R (© The R Foundation for Statistical Computing). It is also possible
184 to apply generalized linear mixed models (GLMM), examining different sources
185 of literature as a random factor (Dormann et al. 2007), which may be considered
186 a standard for meta-analysis. In this way, we can only control the spatial
187 autocorrelation within each source of data. However, we chose GLS rather
188 than GLMM because (1) according to the preliminary analysis, these two
189 methods provided essentially the same results and (2) we consider it necessary
190 to control the spatial autocorrelation not only within the same study but also
191 between the study sites derived from different sources of data.
192
193 Frugivore diversity

194 Stevenson (2001) showed that fruit fall significantly affected the richness of
195 primate species among 13 Neotropical primate communities. We added data
196 of six sites in Asia and Africa by reviewing the literature on primate diversity.
197 Since only Japanese macaques are distributed throughout Japanese
198 archipelago, Japanese data (N=11) are not independent of each other due to the
199 isolated location and unique primate biogeography. Therefore, for our analysis
200 of the effect of fruit fall on primate diversity, we included only one Japanese site,
201 where the fruit fall was the median value among sites in Japan. In this analysis,
202 we included not only strictly frugivorous primates but also seed predators and
203 partial frugivores, such as howler (*Alouatta*) and colobus monkeys (*Presbytis*,
204 *Colobus,* etc.); therefore, all non-tarsier haplorhini primates (anthropoids) were
205 included. Most of these primates consume at least some parts of fruit fall, such
206 as pulp, seeds, and unripe fruits.
207 Data on the number of frugivorous bird species were reviewed from the
208 literature. We included studies based on systematic observational sampling,
209 covering more than one year, such as point or line transect census. A bird
210 checklist based on long-term accumulation of observational data was available
211 for some sites, but it was not analyzed because it inevitably included very rare
212 birds. We did not use any online distribution database covering a large
213 geographical region (e.g. continent) because data on fruit fall are very local, and
214 the scale of distribution data from these databases was too coarse.
215 'Frugivores' also included partial frugivores and granivores. Dietary
216 classification followed each study, and when classification was not available in
217 the original literature, we followed the distinctions of Kissling *et al*. (2009).
218 For both primate and bird analyses, we examined three types of GLS

models using (1) fruit fall, (2) temperate/tropical classification, and (3) both fruit fall and temperate/tropical classification as (an) independent variable(s). We selected the best-fit model having the smallest AIC. We also analyzed models using absolute latitude rather than temperate/tropical classification, but the results were the same.

Results

Effects of location on fruit fall

Fruit fall generally decreased from tropical to temperate forests, with the exception of the high fruit fall in Australia. When all data were used, the best-fit model included region (whether Australia or not), absolute latitude and altitude (Table 2a, Fig. 1). Fruit fall was larger in Australia (812±461 kg/ha/year, average±SD) than in other regions (Africa: 446±268, America: 411±208, Eurasia: 297±271). When Australia was excluded, the best-fit model included only latitude, indicating fruit fall decreases with increasing absolute latitude (Fig. 1). Fruit fall in tropical forest, temperate forests excluding Australia, and temperate forests including Australia were 454±258, 265±227, and 362±352 kg/ha/year, respectively.

In temperate forest, fruit fall generally decreased with increasing absolute latitude and altitude, with the exception of high fruit fall in Australia. In tropical forest, no location factor affected fruit fall significantly. In temperate forest, the best-fit model included region (whether Australia or not), latitude and altitude (Table 2a). When Australia was excluded, the best-fit model included both latitude and altitude.

244 Effects of climate on fruit fall

245 Fruit fall was larger when annual temperature was higher in the entire dataset
246 and temperate dataset, but no climate factor affected fruit fall in tropical forests
247 (Table 2b). In the entire dataset (both when Australia was excluded and
248 included), the best-fit model included only annual temperature. In temperate
249 forest, the best-fit model included annual temperature and actual
250 evapotranspiration, but only annual temperature was significant. When
251 excluding Australia, the best-fit model included only annual temperature. The
252 R^2 value of climate models was smaller than that of location models when
253 Australia was included, indicating that the peculiarity of Australia cannot be
254 explained by its climate.

255

256 Effects of total litterfall on fruit fall

257 The positive effect of total litterfall on fruit fall was consistent in any kind of
258 dataset (Table 2c, Fig. 2). When Australia was excluded, the R^2 values of the
259 litterfall model were higher than those of location and climate models, in
260 particular in tropical forests (72% in litterfall, 3.1% in location, and 0.6% in
261 climate models). The fruit fall/litterfall ratio did not differ significantly between
262 temperate and tropical forests (tropical forests: 5.6±5.2%, temperate forests:
263 7.6±5.4%; t=1.07, p=0.29). However, the fruit fall/litterfall ratio in Australia
264 (12.6±4.0%) was significantly higher than in other regions (t=3.89, p=0.0004).

265

266 Effects of fruit fall on frugivore diversity

267 Both fruit fall and temperate/tropical classification affected frugivorous primate
268 diversity significantly (Fig. 3), but only temperate/tropical classification affected

bird diversity (Fig. 4). In the case of frugivorous primate diversity, model fitness was better when including both fruit fall and temperate/tropical classification (AIC=90.2, R^2=0.61, p=0.00055) than when including only one of them. The increase in AIC was larger when removing temperate/tropical classification (5.62) than when removing fruit fall (1.50), indicating that the effect of temperate/tropical classification was larger than that of fruit fall. In the case of frugivorous bird diversity, none of the models was significant; however, model fitness was higher when including only temperate/tropical classification (AIC=63.3, R^2=0.36, p>0.10) than when including only fruit fall or both.

Discussion

Variations in fruit fall around the globe

We found that the difference in fruit fall between temperate and tropical forests was significant, and this difference was 1.71 times larger when highly fruit-rich Australia was excluded. Fruit fall in Australia was, on average, more than two times higher than that in other regions. The two high values in Australia were derived from a five-year study (Lowman 1988), so it is unlikely that the high fruit fall was just a by-product of a mast fruiting year. Five out of the six Australia datasets were derived from one study (Lowman 1988), so the Australian data may have been affected by methodological differences that were not described explicitly in the paper. High fruit fall in Australia remains a preliminary conclusion that needs to be tested by more studies.

The difference between temperate and tropical forests was only two times or less, which is comparable that of plant productivity (Pärtel et al. 2007) but much smaller than that predicted by Moles *et al*. (2009). Moles *et al*. (2009)

294 predicted that the difference in mass of seed rain between the equator and the
295 latitude of 35º was 4-70 times, based on seed rain density and average seed
296 size. The result was the same even when only forests were analyzed. The
297 likely reason is that their estimation was based on the assumption that all the of
298 species equally contribute to the total fruit fall/seed rain. Since there is a huge
299 variation in seed size within the same area (Moles et al. 2007), if the fruit (seed)
300 fall is represented disproportionately by a few very large species in temperate
301 forests, it is understandable that the temperate/tropical difference becomes
302 smaller than they estimated. In fact, in Yakushima, southern Japan, the five
303 most abundant species (*Abies firma*, *Quercus salicina*, *Tsuga sieboldii*,
304 *Cryptomeria japonica* and *Stewartia monadelpha*) were 2nd, 3rd, 5th, 10th, and 15th
305 in unit weight, respectively, among the 51 species which constituted at least
306 0.1% of the fruit fall in at least one of the five plots (G. Hanya & S. Aiba,
307 unpublished data). Considering that these genera, except *Stewartia*, are
308 usually dominant in temperate forests (Hendrick 2001), fruit fall in temperate
309 forests may be represented disproportionately by these large-fruited/seeded
310 species. Consequently, the difference in total fruit fall between temperate and
311 tropical forests becomes moderate (ca twice or less), not 4-70 times.
312
313 Factors affecting fruit fall
314 Our analysis strongly suggests that primary production is the direct determining
315 factor of fruit production. Since the R^2 values in the litterfall model were larger
316 than those of location and climate models, excluding Australia, location and
317 climate affected fruit fall only indirectly by way of primary production. The fruit
318 fall/litterfall ratio did not vary between temperate and tropical forests. Since

litterfall can be regarded as a proxy of primary production in primary forests (Aiba et al. 2007), the relative reproductive output by plants (compared with their primary production) does not seem to vary with latitude. However, again, Australia was an exception to this tendency. Even within Australia, there was a tendency for fruit fall to increas with increasing litterfall ($r=0.79$, $z=1.85$, $p=0.064$), although the sample size was not large enough to examine statistically. Therefore, the same mechanism also seems to work in Australia, although the slope of the fruit fall/litterfall relationship may differ between Australia and the other regions.

Annual temperature was a better predictor of fruit fall than precipitation or evapotranspiration. This was unexpected because evapotranspiration is the best climatic predictor of primary production (Rosenzweig 1968). The resolution of evapotranspiration data was very low (0.5º latitude/longitude, a square of approximately 67 km × 67 km at a latitude of 36º). On the other hand, temperature data were available for each particular site, and even if we derived data from a nearby meteorological station, we incorporated the effects of altitude by assuming the temperature lapse rate. The most likely scenario is that temperature limits evapotransporation, evapotransporation limits primary production (Leith 1975), which, in turn, limits fruit fall. Evapotransipiration does not increase linearly with precipitation, so the production- and/or fruit fall-precipitation relationship should be only weakly linear. In fact, we did not detect an effect of precipitation in any of the datasets. Temperature is not a limiting factor in tropical forests, so a single climate factor is only a weak predictor of fruit fall within tropical forests. Precipitation is sometimes used as a proxy of food availability for frugivores (Chapman and Balcomb 1998), but we

344 did not find a significant effect on fruit fall. The reason might be because the
345 data were biased to humid regions, including only one site having annual
346 precipitation <1000 mm. This site (Mana Pools, Zimbabwe) had a relatively
347 small fruit fall (300 g/ha/year) (Dunham 1989), and thus rainfall may have a
348 positive effect on fruit fall when data on dry forests are included.
349
350 Implications for frugivore diversity
351 The effect of fruit fall on diversity was different between the two types of
352 frugivores (primates and birds). For primates, fruit fall seemed to explain some
353 of the variations in diversity. However, there remained variations in primate
354 diversity between temperate and tropical forests which cannot be explained
355 solely by fruit fall, since not only fruit fall but also temperate/tropical classification
356 was included in the best-fit model. On the other hand, no relation between bird
357 diversity and fruit fall was detected, although bird diversity was higher in the
358 tropics, even with this limited dataset (Fig. 4). This difference resulted from the
359 migration habit of birds, which makes it difficult to relate bird diversity with total
360 annual fruit production.
361 In the case of primates, the fruit fall-diversity relationship, which
362 explained at least part of the higher diversity in the tropics, is probably mediated
363 by biomass and/or number of individuals (population density). It is known that
364 annual fruit fall also affects primate biomass and density (Stevenson 2001;
365 Hanya et al. 2004). Most primates are residents and stay in a fixed place
366 (home rage) throughout the year, regardless of the seasonal changes in fruit
367 availability. In this situation, when annual fruit production is low, primates need
368 a larger home range to secure foods, thus biomass per unit area becomes low

(Hanya et al. 2006). This reasoning holds true even when fruit availability varies seasonally, either because fruit availability during the fruit-scarce season correlates with annual fruit production or because primates survive the fruit-scarce season by relying on fat deposited during the fruit-rich season (Hanya et al. 2006). Supposing that population size correlates with speciation rate (positively) and extinction rate (negatively), the number of species would increase with an increasing total number of individuals in the community (see Introduction). Tropical forests having higher fruit fall can sustain more primate individuals, thus harboring a higher number of primate species than do temperate forests.

On the other hand, birds can migrate seasonally all over the globe, such as between temperate and tropical regions (Noma and Yumoto 1997). In addition, they often switch their diet between the habitats they migrate to and from. For migrant frugivorous birds, it is understandable that there is no correlation with the number of species and total annual fruit fall, as each species responds to the fruit availability during a particular season. Kissling *et al*. (2007) found a positive relation between fig species diversity and frugivorous bird diversity within the sub-Saharan region (mostly tropical area). As one of the explanations for this tendency, they proposed a ‘resource-abundance hypothesis’, which is essentially the same mechanism as we used to explain primate diversity by fruit fall. Even for birds, high fruit availability may cause high bird diversity on a limited scale, such as within tropical regions of the same continent. However, when explaining the difference between tropical and temperate regions, the problem of migration cannot be neglected, and thus it is impossible to explain higher diversity in tropical regions by total annual fruit fall.

394 Although there may be a correlation when only the number of resident species
395 was analyzed, it was difficult to get reliable information whether the species is
396 migratory or resident based on literature survey.
397 Although fruit fall explained some variations in frugivore diversity
398 between temperate and tropical forests, our analysis suggests that other factors
399 also contribute to higher frugivore diversity in tropical than in temperate regions.
400 In addition to migration and fruiting availability and its seasonality, evolutionary
401 history (see Introduction), higher proportion of fleshy-fruits (Willson et al. 1989),
402 and more diverse species composition (Takyu et al. 2005) in tropical than in
403 temperate forests may also affect higher frugivore diversity in tropical forests.
404 The proportion of fleshy-fruited woody plant species is 82-90% in tropical rain
405 forests and 47-66% in temperate forests (Willson et al. 1989). Therefore, the
406 amount of available food might be larger in tropical forests than suggested by
407 gross fruit fall alone. Since tree species diversity is higher in tropical forests,
408 broader niches are available there for frugivores with respect to fruit size, color,
409 and presentation pattern (height), permitting the coexistence of more species
410 (Kissling et al. 2007). Unfortunately, data on these factors were not available
411 for most of the studies reviewed here; therefore, detailed comparisons
412 (presumably with a limited data set) are required in the future.
413
414 Other possible influencing factors
415 Fruit fall data provide only an indirect measure of fruit productivity because it
416 quantifies the fruits which were not eaten by animals in the canopy. In addition,
417 the fruit trap method may ignore the very small fruits/seeds which pass through
418 fruit traps. In addition, not all fruit parts are edible for frugivores, such as

419 capsular fruits. Therefore, not only the fruit fall but also the type of fruits and the
420 proportion of consumption in the canopy also be taken into account for the future
421 analysis of the effect of fruit availability on frugivore diversity. However, it is
422 known that, even without considering these factors, fruit fall data convincingly
423 explain frugivore abundance (Ganesh and Davidar 1999; Stevenson 2001).
424 Therefore, we assume that the pattern found here reflects the actual pattern in
425 fruit production.
426
427 In conclusion, fruit fall in tropical forests is only 1.71 times larger than that in
428 temperate forests, which is smaller than the difference in frugivore diversity.
429 Primary production seems the most important determining factor of fruit fall.
430 Among climate factors, annual temperature affected fruit fall in the entire dataset
431 and within temperate forests, but no climatic factor affected fruit fall in tropical
432 forests. Fruit fall seemed to explain at least some temperate/tropical difference
433 in frugivorous primate diversity, but not for frugivorous bird diversity.
434
435 **Acknowledgements**
436 We would like to thank our friends and colleagues in Yakushima for their
437 hospitality and help. M. Nakajima, K. Onishi, S. Komizu, M. Nagai, S. Adachi, C.
438 Igari, M. Aoyama, T. Tsuzuki, Y. Nakamura, S. Shimoinaba, K. Nakura, Y.
439 Hanazaki, T. Nishihara, T. Suzuki, A. Kobayashi, M. Judai, Y. Otani, K. Fuse, T.
440 Dan, D. Ishiyama, A. Hosogaki, M. Nishikawa, H. Inoue, M. Nishioka, Y.
441 Yamananashi, and Y. Kanuma assisted us in the field and laboratory. Dr. H.
442 Enari assisted us to analyze data on evapotranspiration. Dr. P. Stevenson
443 offered us valuable information on his published paper. The Sarugoya

444 Committee and former Field Research Center of Primate Research Institute,
445 Kyoto University (KUPRI) (presently, Wildlife Research Center) offered us
446 excellent facilities. The Yakushima Forest Environment Conservation Center
447 and Kirishima-Yaku National Park gave us permission to study in the area. We
448 are grateful to these people and organizations. This study was financed by the
449 Cooperation Research Program of KUPRI and the MEXT Grant-in-Aid for JSPS
450 Fellows, the 21st Century COE Program (A14) and Global COE Program
451 “Formation of a Strategic Base for Biodiversity and Evolutionary Research: from
452 Genome to Ecosystem.”

453

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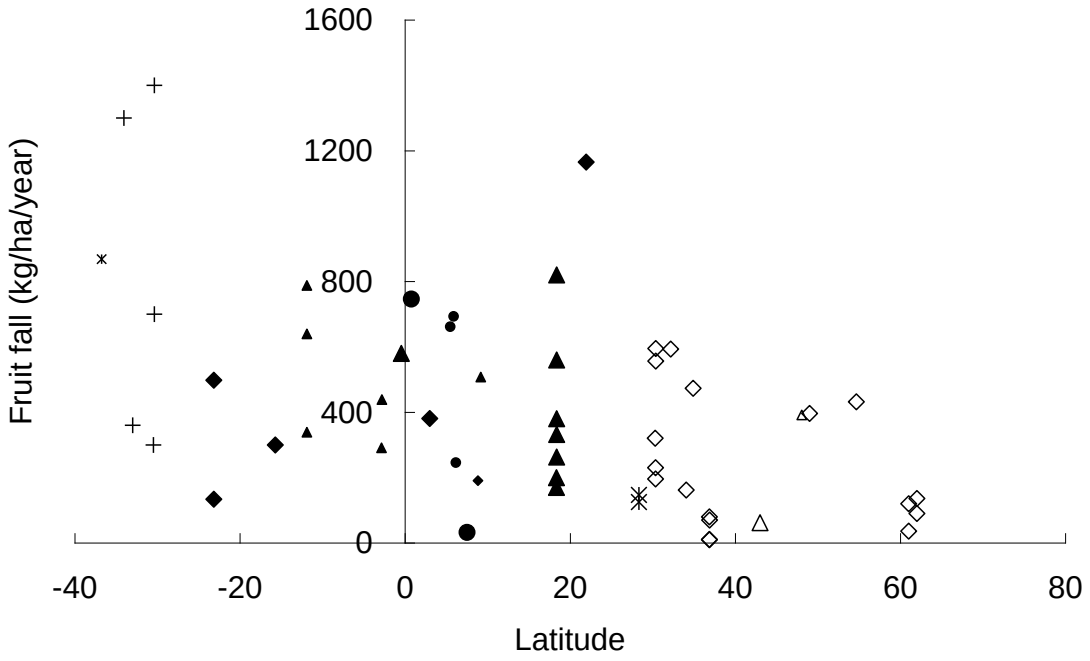
628 Legend to the figures

629 Fig. 1. Latitudinal variations in fruit fall. Diamond: Eurasia, triangle: America,
630 circle: Africa, cross: Australia, asterisk: other (Canary Islands and New
631 Zealand). Open symbols indicate temperate forests and closed symbols
632 indicate tropical forests. Small symbols indicate that the dry weight of fruit
633 was estimated either by the wet weight (by multiplying 0.295) or by the total
634 weight of fruit and flower. Data in Yakushima are authors' unpublished data.
635 Other sources: (Bray and Gorham 1964; Bernhard 1970; Smythe 1970; John
636 1973; Tagawa 1973; Satoo et al. 1977; Kira 1978; Terborgh 1983; Furuno
637 1986; Lowman 1988; Dunham 1989; Morellato 1992; Lugo and Frangi 1993;
638 Muoghalu et al. 1993; Saito 1993; Chapman et al. 1994; Sanchez and
639 Alvarez-Sanchez 1995; Zhang and Wang 1995; Enright 1999; Ganesh and
640 Davidar 1999; Rodrigues et al. 2001; Edmonds and Murray 2002; Zheng et al.
641 2006; Arévalo et al. 2007; Barlow et al. 2007; Astel et al. 2009).
642 Fig. 2. Relationship between total litterfall and fruit fall. See Fig. 1 for
643 symbols.

644 Fig. 3. Relationship between fruit fall and frugivorous primate diversity.
645 Primate data from Stevenson (2001), Fleagle *et al*. (1999) and Hanya *et al*.
646 (2005). See Fig. 1 for symbols.
647 Fig. 4. Relationship between fruit fall and frugivorous bird species richness.
648 Bird data from Noma &Yumoto (1997), Hanya *et al*. (2005), Estrada *et al.*
649 (1997), Wang & Young (2003), Lock & Naiman (1998), Sekercioglu (2002),
650 Robinson *et al.* (2000) and Carrascal *et al.* (2008). See Fig. 1 for symbols.
651



652

653 Fig. 1

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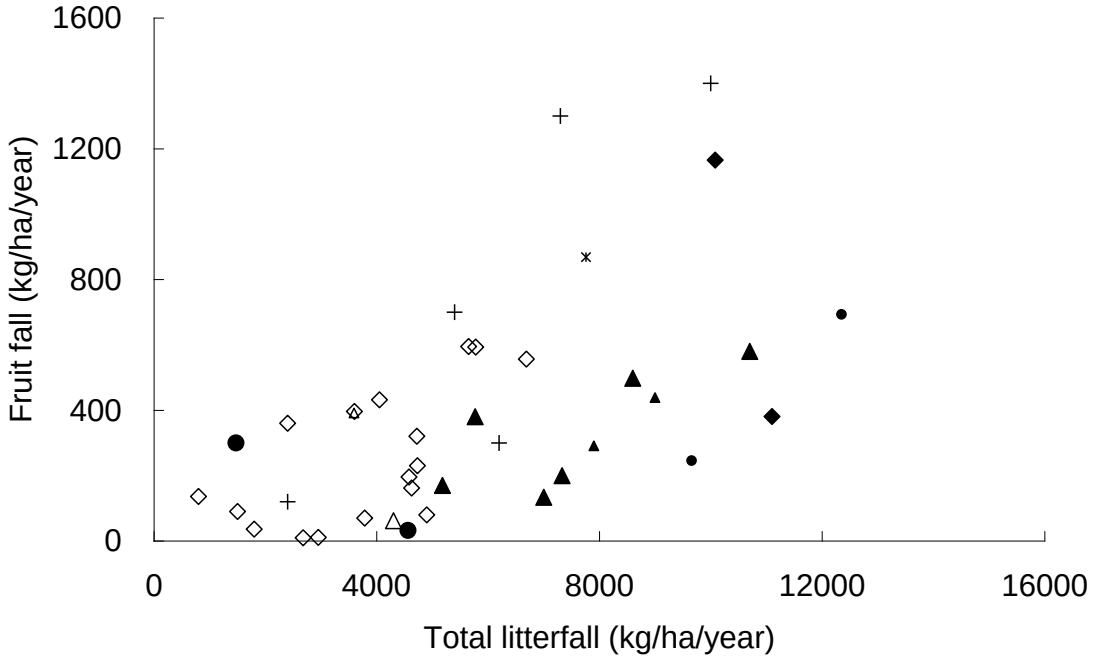

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656 Fig. 2

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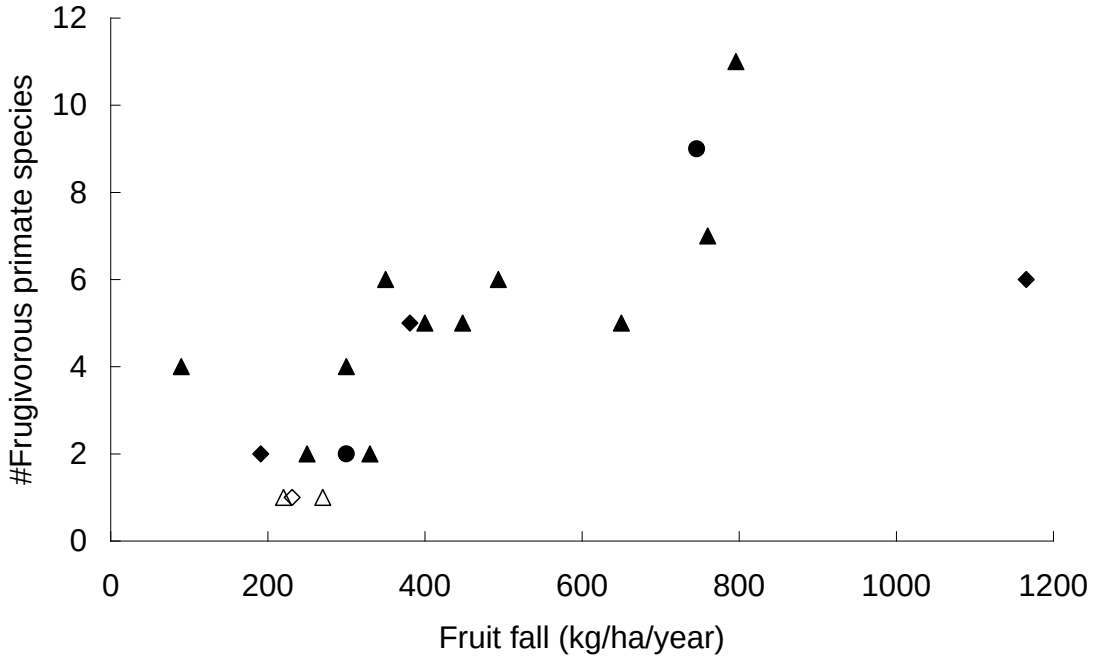

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659 Fig. 3

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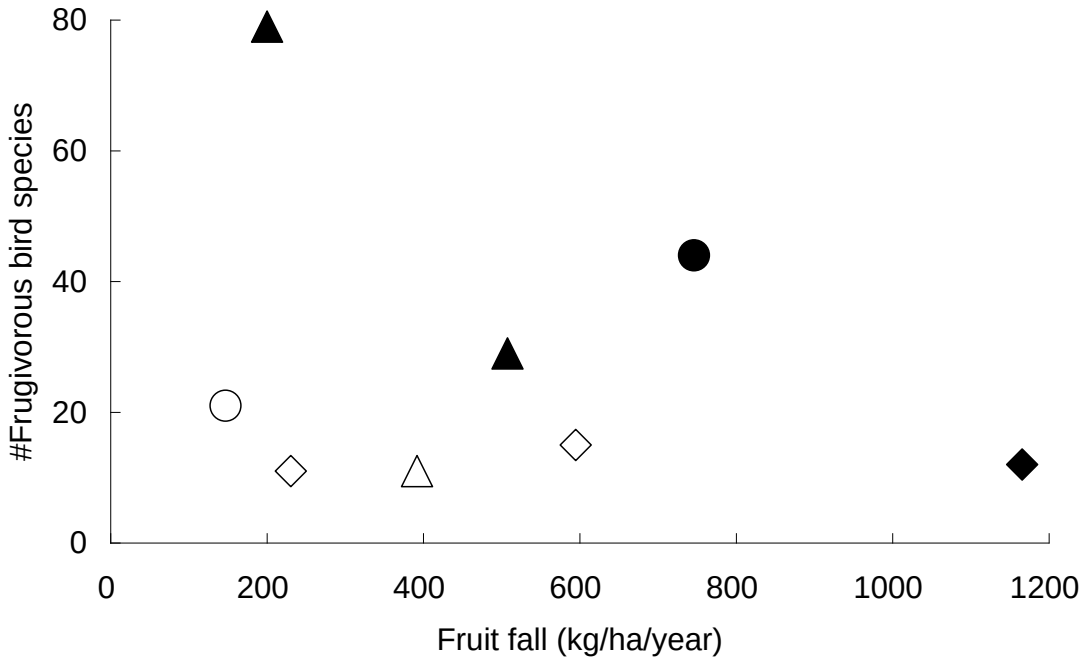

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662 Fig. 4

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Table 1. List of study sites.

Site	Country	Region	Latitude	Longitude	Altitude	Fruit fall	Source
Jari landholding	Brazil	America	-0.5	-51.5	100	580	Barlow et al., 2007
Kibale	Uganda	Africa	0.8	32.4	1500	746	Chapman *et al.* , 1994
Pasoh	Malaysia	Eurasia	3.0	102.3	60	381	Kira, 1978
Ducke (primary forest)	Brazil	America	-2.9	-60.0	72	291	Rodrigues *et al.* , 2001
Ducke (secondary forest)	Brazil	America	-2.8	-59.9	72	439	Rodrigues *et al.* , 2001
Kade	Ghana	Africa	6.2	-0.9	127	246	John, 1973
Ile-Ife(base community)	Nigeria	Africa	7.5	4.5	410	32	Muoghalu *et al.* , 1993
Banco	Ivory Coast	Africa	5.9	-4.0	50	693	Bernhard, 1970
Yapo	Ivory Coast	Africa	5.5	-4.0	50	662	Bernhard, 1970
Kakachi	India	Eurasia	8.8	77.5	1300	191	Ganesh & Davidar, 1999
Barro Colorado Island	Panama	America	9.2	-79.8	40	507	Smythe, 1970
Cocha Coshu (forest)	Peru	America	-11.9	-71.4	400	339	Terborgh, 1983
Cocha Coshu (levee)	Peru	America	-11.9	-71.4	400	640	Terborgh, 1983
Cocha Coshu (river)	Peru	America	-11.9	-71.4	400	788	Terborgh, 1983
Luquillo (palm flood plain)	Puerto Rico	America	18.4	-65.7	300	560	Lugo & Frangi, 1993
Luquillo (lower montane forest)	Puerto Rico	America	18.4	-65.7	300	332	Lugo & Frangi, 1993
Luquillo (secondary forest)	Puerto Rico	America	18.4	-65.7	600	820	Lugo & Frangi, 1993
Luquillo (upper montane forest)	Puerto Rico	America	18.4	-65.7	1000	263	Lugo & Frangi, 1993
Los Tuxtlas (forest1)	Mexico	America	18.4	-95.3	120	380	Sanchez & Alvarez-Sanchez, 1995
Los Tuxtlas (forest2)	Mexico	America	18.3	-95.3	120	200	Sanchez & Alvarez-Sanchez, 1995
Los Tuxtlas (secondary forest)	Mexico	America	18.3	-95.3	120	170	Sanchez & Alvarez-Sanchez, 1995
Mana Pools	Zimbabwe	Africa	-15.7	29.4	360	300	Dunham, 1989
Xishuangbanna	China	Eurasia	21.9	101.2	650	1166	Zheng *et al.* , 2006
Japi Mountains (tropical semideciduous forest)	Brazil	America	-23.2	-46.9	870	498	Morellato, 1992
Japi Mountains (tropical semideciduous altitudinal for	Brazil	America	-23.2	-46.9	1170	134	Morellato, 1992
Canary Islands (Aguirre)	Spain	CI	28.3	-16.6	850	147	Arévalo *et al.* , 2007
Canary Islands (El Moquinal)	Spain	CI	28.3	-16.6	820	125	Arévalo *et al.* , 2007
Yakushima (W280)	Japan	Eurasia	30.4	130.4	280	595	Hanya & Aiba, unpublished
Yakushima (W1050)	Japan	Eurasia	30.3	130.5	1050	231	Hanya & Aiba, unpublished
Yakushima (E170)	Japan	Eurasia	30.4	130.6	170	557	Hanya & Aiba, unpublished
Yakushima (E570)	Japan	Eurasia	30.3	130.6	600	196	Hanya & Aiba, unpublished
Yakushima (E1200)	Japan	Eurasia	30.3	130.6	1200	320	Hanya & Aiba, unpublished
New England NP	Australia	Australia	-30.5	152.4	1200	300	Lowman, 1988
Dorrigo NP (SNVF)	Australia	Australia	-30.4	152.7	800	700	Lowman, 1988
Dorrigo NP (CNVF)	Australia	Australia	-30.4	152.7	800	1400	Lowman, 1988
Minamata	Japan	Eurasia	32.2	130.4	600	593	Tagawa, 1973
Dwellingup	Australia	Australia	-33.0	116.0	270	360	Bray & Gorham, 1964
Wakayama	Japan	Eurasia	34.1	135.6	700	162	Furuno, 1986
Uji	Japan	Eurasia	34.9	135.8	90	473	Saito, 1993
Royal NP	Australia	Australia	-34.1	151.1	20	1300	Lowman, 1988
Naeba	Japan	Eurasia	36.9	138.8	650	70	Satoo, 1977
Naeba	Japan	Eurasia	36.9	138.8	900	80	Satoo, 1977
Naeba	Japan	Eurasia	36.9	138.7	1300	10	Satoo, 1977
Naeba	Japan	Eurasia	36.9	138.7	1500	11	Satoo, 1977
Hupai Scientific Researve	New Zealand	NZ	-36.8	174.7	66	868	Enright, 1999
Wisconsin	USA	America	43.0	-89.0	290	62	Bray & Gorham, 1964
Olympic NP	USA	America	48.1	-123.4	500	392	Edmonds & Murray, 2002
-	Czechoslovakia	Eurasia	49.0	18.0	237	396	Bray & Gorham, 1964
Slowinski NP	Poland	Eurasia	54.7	17.3	20	432	Astel et al., 2009
Evo, *Pinus*	Finland	Eurasia	61.0	25.0	105	36	Bray & Gorham, 1964
Evo, *Picea*	Finland	Eurasia	61.0	25.0	105	120	Bray & Gorham, 1964
Hirkjolen, *Picea*	Norway	Eurasia	62.0	10.0	800	90	Bray & Gorham, 1964
Hirkjolen, *Pinus*	Norway	Eurasia	62.0	10.0	800	136	Bray & Gorham, 1964

664 Minus values in latitude and longitude indicate southern and western hemisphere, respectively.

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Table 2. Best-fit models on fruit fall in generalized least squares (GLS) regression

(a) Location

Examined data	Adopted factors	AIC	R^2
Tropical+Temperate	**Region (Australia)+, absolute latitude-**	683	0.33
Tropical+Temperate (excluding Australia)	**Absolute latitude-**, region (Eurasia)	609	0.26
Tropical	Absolute latitude+, region (Eurasia)-, region (America)-	340	0.027
Temperate	**Region (Australia)+, altitude-, absolute latitude-**	337	0.61
Temperate (excluding Australia)	**Absolute latitude-, region (New Zealand)+**	256	0.38

(b) Climate

Examined data	Adopted factors	AIC	R^2
Tropical+Temperate	**Annual temperature+**	743	0.12
Tropical+Temperate (excluding Australia)	**Annual temperature+**	651	0.23
Tropical	Annual temperature+	341	0.0002
Temperate	**Annual temperature+**, actual evapotranspiration+	383	0.24
Temperate (excluding Australia)	**Annual temperature+**	288	0.36

(c) Litterfall

Examined data	Adopted factors	AIC	R^2
Tropical+Temperate	**Litterfall+**	545	0.32
Tropical+Temperate (excluding Australia)	**Litterfall+**	456	0.33
Tropical	**Litterfall+**	196	0.28
Temperate	**Litterfall+**	336	0.64
Temperate (excluding Australia)	**Litterfall+**	257	0.36

Bold indicates significant factors.
+ means that the factor had a positive effect and - means that the factor had a negative effect on fruit fall.